

Plant VOCs emission: a new strategy of thermotolerance

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Abstract: Plant leaves may emit a substantial amount of volatile organic compounds (VOCs) into the atmosphere, which include isoprene, terpene, alkanes, alkenes, alcohols, aldehydes, ethers, esters and carboxylic acids. Furthermore, most of these compounds actively participate in tropospheric chemistry. Great progresses have been made in linking emission of these compounds to climate. However, the VOCs emission function in plant is still not clear. Recently, some evidence has emerged that the production and the emission of VOCs, such as isoprene and monoterpenes, which account for 80% of total VOCs, exhibit plant protection against high temperatures. These increases in VOCs emissions could contribute in a significant way to plant thermotolerance. This perspective summarizes some latest literatures regarding the VOCs emission-dependent thermoprotection in plant species subjected to high temperature stress, presents the achievement in studies concerning plant VOCs emission-dependent thermotolerance, and then exhibits the proposed mechanisms of such plant thermotolerance. Finally, open questions regarding the plant VOCs emission were shown, and the future researches were proposed.

Keywords: Volatile Organic Compounds (VOCs); Isoprene; Monoterpene; Photosynthesis; Thermotolerance; Thermoprotection

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Introduction

Plants, especially plant species grown in the tropical region, re-emit a substantial fraction of their assimilated carbon into the atmosphere as volatile organic compounds (VOCs). These VOCs represent a large carbon loss and can be up to 10% of that fixed by photosynthesis under stressful conditions and up to 100 g·C m⁻² per year in some tropical ecosystems (Peñuelas & Llusà 2003). Moreover, at a global scale, the emissions of plant VOCs exceed by several-fold those emissions from anthropogenic sources (Peñuelas & Llusà 2004). Accordingly, the issue of plant VOCs emission attract scientist from all over the world, who can not help asking themselves such question that why plants emit such large amounts of VOCs? The question of VOCs emission function in plant always challenges scientists in past years. Recently, regarding the function of the plant VOCs emission, there have existed many hypotheses, such as plant thermotolerance, plant antioxidation, and plant protection against herbivore, which attempt to answer this question that why plant emit VOCs. However, plant VOCs emission-dependent thermotolerance against high temperature has received considerable attention in the past score years. To this day, there have been reports, showing that plant VOCs emissions can pay an important role in plant thermoprotection from high temperature. Consequently, researchers increasingly debate that, since plant VOCs emission exert thermoprotection from high temperature, whether or not can we make such a conclusion that plant VOCs emission is a new strategy of thermotolerance?

VOCs are produced in many different plant tissues and physiological processes. They are diverse, including isoprene, monoterpene, alkanes, alkenes, alcohols, esters, carbonyls and

acids. However, of importance for atmospheric chemistry are mainly the more volatile compounds isoprene and monoterpene, both of which were often used to examine plant VOCs emission-dependent thermoprotection function in plant species. Actually, it was concluded that both isoprene and monoterpene account for 80% of total plant VOCs. Moreover, all the conclusions regarding plant VOCs emission thermoprotection in plant species derive from experimental results by fumigation with either isoprene or monoterpene.

Isoprene and monoterpene

Isoprene (2-methyl-1, 3-butadiene) is emitted by a variety of plant species and exerts profound effects on atmospheric chemistry (Harley *et al.*, 1999; Logan *et al.*, 2000). However, not all plants emit isoprene. Most that do are woody in growth habit, and the species with the highest emission rates are found in the genera *Quercus* (oaks) and *Populus* (poplars) (Harley *et al.*, 1999). Among conifers, only *Picea* (spruces) are emitters, and they emit at only moderate rates. The biochemical and physiological controls over the production of isoprene have received considerable attention in the past ten years because of the discovery of a novel biosynthetic pathway and the emergence of hypotheses concerning the possible adaptive role of isoprene during heat stress (Sharkey & Singsaas 1995; Singsaas *et al.*, 1997). This field is currently in a state of intellectual adjustment as biochemical discoveries are integrated with past experimental observations. Isoprene emission is different emission of the related and better known monoterpenes, isoprene emission requires de novo synthesis. However, emission of monoterpenes is, in most cases, from pools of hydrocarbon stored in resin ducts, glands, or trichome (Sharkey and Yeh 2001)

Monoterpenes constitute a major fraction of the plant VOCs emitted from vegetation (Guenther *et al.*, 1995) and serve a wide range of functions in plant. In particular, the conifers, mint, citrus, and composite families accumulate these substances in ducts, glands and cavities. These isoprenoids are considered a means of defence against insects, fungi, herbivores and other plant species. When volatilized, monoterpenes can be signals for pollinators

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and conspecific herbivores, and can also mediate tritrophic interactions (Harborne, 1991). However, recent observations indicate that leaves of several tree species, such as the evergreen sclerophyllous holm oak (*Quercus ilex*), emit large amounts of monoterpenes despite the absence of storage pools (Loreto *et al.*, 1998a). As demonstrated for isoprene (Sharkey & Yeh, 2001), this monoterpene emission is largely associated with photosynthesis. It is stimulated by light, declines in the dark, and is inhibited in the absence of atmospheric CO₂ (Loreto *et al.*, 1996a,b). The physiological function of the emission of nonstored monoterpenes from certain plant species is a matter of debate and an important topic of current research on biosphere-atmosphere exchange. In this respect, one of the most fascinating hypotheses is that monoterpenes may protect leaves against high-temperature damage (Sharkey & Singsaas, 1995; Loreto *et al.*, 1998a; Delfine *et al.*, 2000; Peñuelas & Llusià 2002). Even though this phenomenon has been demonstrated for several species, clear-cut evidence for the proposed mechanisms of this profound effect has not been achieved (Sharkey & Yeh, 2001).

The thermotolerance hypothesis

Sharkey and Singsaas (1995) were the first people to propose that isoprene has a thermotolerance function. Holding leaves in darkness or in a nitrogen atmosphere to control endogenous isoprene synthesis, researchers assessed damage to photosynthesis as the temperature at which chlorophyll fluorescence increased (Seemann *et al.*, 1984). Singsaas *et al.*, (1997) showed that adding isoprene to an air stream (or nitrogen gas) that passed over these leaves could increase the temperature at which damage occurred from as low as 35 °C to as high as 45°C. These experiments indicated that isoprene was having some effect on the temperature tolerance of photosynthesis. Actually, earlier work had already suggested that isoprene biosynthesis was linked to photorespiration (Jones & Rasmussen 1975). However, subsequent results with *Populus tremuloides* (Monson & Fall 1989), or *Arundo donax* (Hewitt *et al.*, 1990), among others, did not find such a relationship. Nevertheless, the most recent studies have not just focused on photorespiration as an alternative source of carbon for isoprenoid biosynthesis when photosynthesis is limited.

Fortunately, direct tests of the thermotolerance hypothesis became possible when it was discovered that fosmidomycin, an inhibitor of the isoprene synthesis pathway (Zeidler *et al.*, 1998) was highly specific and did not inhibit photosynthesis (Sharkey *et al.*, 2001). Following three heat spikes (2 min at 42 °C), photosynthesis at 30°C was inhibited by one-third when leaves were able to make isoprene but by two-thirds when isoprene production was inhibited. Exogenous isoprene given to fosmidomycin-fed leaves could restore thermotolerance (Sharkey *et al.*, 2001). The latest research (Peñuelas *et al.*, 2005) reports that isoprene fumigation of *Quercus ilex*, which normally does not emit isoprene, result in substantial thermotolerance between 35 and 45 °C, and photosynthesis at 50 °C was depressed to the same degree in both treatments. Velikova and Loreto report that exposing leaves of *Phragmites australis* to 38 °C for 90 min caused a greater reduction in photosynthesis when isoprene synthesis was inhibited by fosmidomycin, than when it was not (Velikova & Loreto 2005). In addition, photosynthesis recovered more when the leaf temperature was returned to the pre-stress level of 30°C when isoprene was present than when it was inhibited

(Sharkey 2005). Thermotolerance is much easier to see during the recovery from heat stress than during the initial heat stress episode (Sharkey *et al.*, 2001; Velikova & Loreto 2005). Isoprene-induced thermotolerance is very fast (Singsaas & Sharkey 1998; Singsaas *et al.*, 1999) compared with changes in xanthophyll (Havaux *et al.*, 1996) or fatty acid composition of thylakoid (Murakami *et al.*, 2000). These results show that isoprene synthesis and emission provide tolerance of short high-temperature episodes. In fact, so far the thermotolerance hypothesis for isoprene emission function now has substantial support, given three independent reports using different species and methods (Sharkey *et al.*, 2001; Peñuelas *et al.*, 2005; Velikova & Loreto 2005).

The recognition that monoterpene synthesis increases dramatically at high temperatures and that this can cause them to build to high concentrations in tissues led to the hypothesis that emitted monoterpene may protect plants from temperature. To study thermotolerance caused by monoterpenes, Loreto *et al.*, (1998b) fumigated terpene-emitting *Quercus ilex* leaves with a mixture of five monoterpenes during heat treatments and showed a significant stimulation of photosynthesis at high temperatures over unfumigated leaves. To complement the studies with *Quercus ilex*, Delfine *et al.*, (2000) have tested whether terpene fumigation affects thermotolerance in a species that does not itself make terpenes, *Quercus suber*, by fumigation with a mixture of monoterpenes. They first showed that fumigation with exogenous terpenes resulted in increased terpene levels inside the leaves, and then demonstrated a significant increase in photosynthesis at elevated temperatures. This is more evident when leaves were given more than one high temperature treatment. Thus, researchers conclude that thermotolerance could be increased in a non-emitting species by fumigating with exogenous monoterpenes. Furthermore, monoterpene emitted in a light-dependent manner also provide the same type of thermotolerance as isoprene. Recent research shows a possible link of both monoterpene emission and monoterpene synthesis with photorespiration (Peñuelas & Llusià 2002). Peñuelas and Llusià have shown the formation of monoterpenes might depend on photorespiratory activity, and that under non-photorespiratory conditions monoterpene seem to replace photorespiration in providing protection against high temperatures (Peñuelas & Llusià 2002). Repeated cycles of high-temperature stress give reduced recovery in leaves without isoprene and monoterpene, although leaves with isoprene or monoterpene maintain high rates of photosynthesis, especially after repeated periods of high temperature (Delfine *et al.*, 2000; Loreto *et al.*, 1998b; Sharkey *et al.*, 2001). More and more evidence show VOCs emission may protect plant from high temperature stress, which plant species, especially tropical plant species, often suffer from. However, the really intrinsic mechanism of plant VOCs emission-dependent thermotolerance is still poorly understood to this day. So this issue deserves comprehensive research.

The proposed mechanisms of thermotolerance

What is the intrinsic mechanism of the plant VOCs emissions providing thermotolerance? Speculation concerning the mechanism by which isoprene protects against short high-temperature episodes depends upon characteristics of the high temperature damage. An attractive idea for which data exists is that thylakoid membranes become leaky at moderately high temperature (Buk-

hov *et al.*, 1999; Pastenes & Horton 1996). Isoprene could reside in the thylakoid membrane for a short time and enhance hydrophobic interactions. It could even block the formation of water channels because of the large volume of the double bonds. Another alternative is that high temperature excursions could allow large membrane-bound protein complexes (e.g. photosystem II) to fragment. Isoprene could enhance hydrophobic interactions within either membranes or protein complexes. Because each excursion to high temperature could result in more nonbilayer structures or more disrupted protein complexes, repeated high temperature episodes would progressively reduce the photosynthetic capacity. As leaves can be subject to dozens of high-temperature episodes each day (Singsaas *et al.*, 1999; Singsaas & Sharkey 1998), the increased recovery from each episode afforded by isoprene could become very important to the plant. However, the above mentioned mechanisms for plant VOCs emissions thermoprotection has not received direct evidence.

Interestingly, Singsaas (2000) proposed that the intrinsic mechanism of VOCs emission-dependent thermotolerance is the same as that of xanthophyll-induced thermotolerance. The ion permeability of the thylakoid membranes increases at high temperature. This is compensated for by increasing cyclic photophosphorylation around photosystem II (Bukhov *et al.*, 1999). If temperature continues to rise, the cyclic photophosphorylation cannot keep up with the proton leakage and the transmembrane gradient drops, causing a reduction in ATP synthesis. This can inhibit RuBP regeneration and lower the Rubisco activation state (Robinson & Portis 1988). Reducing proton leakage will delay this chain of events. When zeaxanthin is present in the membranes, proton leakage is reduced at high temperatures (Tardy & Havaux 1997). One hypothesis is that zeaxanthin may act as a solute in the membrane, which stabilizes its structure at high temperature. Since VOCs are extremely hydrophobic molecules and partition into membranes, they could have similar membrane-stabilizing properties. Nevertheless, the proposed mechanisms of the VOCs emission-dependent thermotolerance have not been widely accepted to this day. Thereby, investigators need much more evidences to reveal the intrinsic mechanism of VOCs emission-dependent thermotolerance.

Conclusions and open questions

In conclusion, among the great variety of likely plant VOCs emissions functions in plants, most recent reports show that plant VOCs emissions could protect plants against high temperatures. Some reports even show that the process of plant VOCs emissions providing thermotolerance is linked to photorespiration (Peñuelas and Llusà, 2002; 2005). The importance of the work by Peñuelas and Llusà is its contribution to our understanding of the possible physiological mechanisms underlying VOCs-related thermotolerance. It demonstrates that photorespiration seems to be necessary to avoid photochemical damage most notably under high temperature conditions. When fumigated with VOCs under nonphotorespiratory conditions, VOCs emission seems to replace photorespiration in the protection against high temperatures. Here, it is emphasized that achievements regarding VOCs emissions thermotolerance function in plant species were obtained from experiments of little plant species, which is either emitter or nonemitter fumigated with VOCs, thus strong and positive evidences will be needed to further assess the plant VOCs emissions-induced thermotolerance.

Inevitably, many questions about VOCs relationships with

plant remain to be solved, especially, regarding plant VOCs emission-dependent thermoprotection. Do plants always protect themselves from over-heating by producing and emitting VOCs? Are there species characteristics, physiological states or environmental conditions that determine this photoprotection? Do the VOCs-emitting plant species tolerate higher temperature than the non-VOCs-emitting plant species?

From the evolutionary standpoint, since VOCs emission protects plant from high temperature, why do some plant species emit neither isoprene nor monoterpene, which were dominant VOCs and confirmed to exhibit thermotolerance of photosynthesis in leaves exposed to high temperature? Why do some plant species “lose” function of VOCs emission-dependent thermoprotection during the course of long-term evolution, and what environmental factors might make them “lose” such function?

Additionally, how to link the VOCs emission-dependent thermotolerance to the well-known xanthophyll cycle-induced thermotolerance? What roles will the two processes play in VOCs-emitting plant species subjected to high temperature stress? Which process is more sensitive to high temperature stress? Whether or not the two processes independently function in the different high temperature stress stage? Finally, how does photorespiration affect VOCs synthesis? Which are the intrinsic molecular mechanisms and the interactions involved? To what extent might VOCs emissions directly cool the plant through physiological or evaporative effects?

Future research

From a physiological standpoint, the most important next step is to clone the VOCs, especially isoprene and monoterpene, synthase gene and study its regulation and effects of environment on regulation. This step will answer question about metabolic regulation and provide tools for the further study of the regulation of VOCs emission capacity. After getting more information from this step, we can understand how environmental factors affect VOCs emission, and then according to global variation of environment, we might estimate the amount of emission of VOCs in the future.

Although there are many reports, people still poorly understand the intrinsic mechanism, thereby, studies are still needed on the underlying mechanisms by which VOCs emissions can protect plant species against high temperature. Actually, whether plant VOCs emission is a new strategy of thermotolerance will depend on a clear understanding of its mechanism. Why do some plant species “lose” such function during the course of evolution, whether are there another strategy of thermotolerance in non-emitters replacing the VOCs emission? Whether are emitter greater thermotolerant than non-emitter? The answers of these questions also depend on the understanding mechanism of VOCs emission-dependent thermotolerance. Furthermore, these studies could lead to new discoveries concerning the effect of high temperature on photosynthesis and thylakoid membranes.

And finally, regarding relationship between the emission of VOCs and climate, whether the increased plant VOCs emissions will cool or warm the environment needs to be determined. Whether the increases in both CO₂ concentration and N deposition enhance VOCs emissions from ecosystem or not needs to be examined. The accurate estimation of VOCs emissions from global ecosystem with progressive increases in global temperature is also needed to forecast the interaction effects of plant VOCs emission on global environment. Therefore, investigators

may make an effort to investigate the above issues.

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